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Multimodal signals, imperfect information, and identification of sex in red-backed salamanders (*Plethodon cinereus*)

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Abstract Theoretical treatments and empirical studies both suggest that signals that occur in multiple sensory modes have superior detectabilities, discriminabilities, and memorabilities. There is also an intuitive link between signal detectability, discriminability, and memorability and the quality of information that is transferred via the signaler. We investigated the role of information quality and sensory modality in the sexual identification of intruding conspecifics by territorial male red-backed salamanders (*Plethodon cinereus*). Our results imply that these salamanders are able to discriminate between intruding male and female conspecifics (based on the allocation of aggression) in bimodal scenarios (vision and olfaction) even under situations in which the information available about the intruders' sexual identities is reduced in quality. In unimodal scenarios (olfaction only), male residents exhibited heightened levels of aggression toward male secretions and reduced levels of aggression toward female secretions. In unimodal scenarios where information pertaining to the sex of the stimulus was reduced in quality, male residents displayed intermediate levels of aggression relative to the responses that male and female stimuli received respectively. Although resident males touched bimodal stimuli significantly more than they touched unimodal stimuli, we were unable to find support for the notion that sensory modality greatly influences how male resident red-backed salamanders allocate aggression toward intruding male versus female stimuli.

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Introduction

Animal communication is often conceptualized as consisting of an animal that transmits a signal (the signaler) and another animal that receives the signal sent by the first animal (the receiver). Because receivers must ultimately process and interpret signals, what has become known as "receiver psychology" (Guilford and Dawkins 1991; Rowe 1999) has received theoretical and empirical consideration. In particular, three aspects of how the physical attributes of a signal interact with a receiver's "psychological landscape" (Guilford and Dawkins 1991) have been of interest to researchers. (1) Detectability is how readily a signal can be perceived from background stimuli. (2) Memorability refers to "how easily a signal can be remembered, or associated with some other relevant stimulus" (Guilford and Dawkins 1991). (3) Discriminability involves the categorizing of a stimulus into one "discrete" class versus another (Guilford and Dawkins 1991).

Another important notion to studies of animal communication is that animals often make decisions based on imperfect information (sensu Nowak 1990; Abrams 1994; Koops and Abrahams 1998; Funk and Tallamy 2000): i.e., information that is incomplete, incorrect, or misinterpreted. There is an intuitive link between signal detection, memorability, and discrimination and imperfect information. For instance, if a signal is not detected, the intended receiver is likely to have incomplete or incorrect information about the signaler's intent, location of predators, or a host of other possible environmental parameters. Similarly, if a receiver has difficulty discriminating between two signals, then the receiver may misinterpret one signal for the other. Finally, if a receiver has difficulty remembering a signal, the receiver may have problems detecting the signal or remembering to which discrete class the signal belongs (i.e., discriminating between the signal of interest and another similar signal).

Rowe (1999) concluded that multicomponent signals, and in particular multimodal signals (i.e., signals that are in more than one sensory modality such as sight and smell), are generally easier to detect, remember, and discriminate than unicomponent and unimodal signals. Rowe's conclusions are based on empirical results from studies involving non-human subjects as diverse as shrimp (Hughes 1996) and birds (Hultsch et al. 1999; Rowe and Guilford 1999).

We used red-backed salamanders (*Plethodon cinereus*: Plethodontidae) to test the efficacy of multimodal signals in sexual discrimination. Red-backed salamanders are small terrestrial caudates that defend territories under rocks and logs in the forests of northeastern North America (Mathis 1991; Petranka 1998). Territorial defense in *P. cinereus* may serve two functions: to ensure access (1) to invertebrate prey during dry periods (Jaeger 1980) and (2) to sites that are suitable for courtship, mating, and egg brooding (Mathis 1991).

Red-backed salamanders advertise and defend their territories via signals that occur primarily in two sensory modes. The first is olfaction. Jaeger et al. (1986) demonstrated that male red-back salamanders avoid burrows marked with the fecal matter of conspecifics but are attracted to burrows marked with their own fecal matter. Chemical signals in red-backed salamanders may also contain information about the status or condition of an individual. For example, McGavin (1978) and Gillette et al. (2000) suggested that red-backed salamanders can discriminate between familiar and unfamiliar conspecifics solely from olfactory cues. Second, red-backed salamanders also transmit visual signals (Jaeger 1984; Jaeger and Schwarz 1991; Jaeger and Forester 1993; Gabor and Jaeger 1999). Of particular importance to territorial defense is the posture "all trunk raised" (ATR), which is associated with aggression (Jaeger 1984).

Jaeger (1984) and Lang and Jaeger (2000) demonstrated that territorial male residents of *P. cinereus* are more aggressive toward male intruders than they are toward female intruders. This implies that males are capable of discriminating between males and females that enter their territories. Using *P. cinereus* as a model, we investigated the influence that imperfect information has on sexual discrimination of intruders by residents. We investigated this problem by attempting to reduce the quality of the chemical information available to resident males about the sexual status of intruders (decreasing discriminability). In experiment 1, resident males met male and female intruders that either were covered in secretions of the opposite sex (treated signal) or were not covered in secretions of the opposite sex (plain signal). These residents, then, had two sensory modalities: olfactory and visual. Experiment 2 eliminated the visual signal by presenting resident male red-backed salamanders with swabs of female secretions, male secretions, and male+female secretions simultaneously. This experiment was conducted to see how behavior patterns change when the signal was reduced from a bimodal (visual and olfactory) signal to a unimodal (olfactory) signal.

Methods

Collection

We collected 170 adult red-backed salamanders (100 males and 70 females) in Giles County, Virginia, USA in a section of Jefferson National Forest that is adjacent to Mountain Lake Biological Station (M.L.B.S.). All of the animals that were used in the following experiments were collected on 29 and 30 March 2002. We did not collect gravid females because visual information about their reproductive status may undermine attempts to reduce the quality of information available to residents about such animals' sexual identities. Likewise, individuals of *P. cinereus* with autotomized tails were not collected because the behavior of residents differs depending on whether or not intruders have autotomized tails (Wise and Jaeger 1998).

Processing, storage, and maintenance

Upon collection, each salamander was temporarily placed in a jar that contained paper towels moistened with spring water. They were then taken back to M.L.B.S. and sexed by checking for the presence of testes, which can be seen through the abdomens of males (Gillette and Peterson 2001). The salamanders were also measured for total length (TL) (length from tip of snout to tip of tail). No animals <57 mm TL were kept (to ensure that all animals were adults: Conant and Collins 1998); we excluded juveniles and neonates from our sample because adults of this species often cannibalize them (Petranka 1998). Then, the salamanders were returned to their jars and transported to the University of Louisiana at Lafayette in a cooler that was packed with ice.

Once in the laboratory, the salamanders were placed in petri dishes (14×1.5 cm) that were lined with coffee filters moistened with spring water. This lining was changed as needed and was moistened with spring water every 2 days. While in the laboratory, the salamanders were fed *Drosophila virilis* weekly, and kept on a 12L:12D light/dark cycle at 17±2°C. Experiment 1 was conducted from May to July 2002, and experiment 2 was conducted from December 2002 to January 2003. Although red-backed salamanders' behavioral patterns may change during the mating season (autumn to early spring: Petranka 1998), such behavioral shifts are likely to be cued by temporal factors such as photoperiod. Because our animals were maintained on constant light cycles and temperatures, it is unlikely that they underwent behavioral shifts due to temporal effects. Nevertheless, any time that we present data on comparisons between experiments, we also present data comparing the baseline behavior of the animals from each experiment.

General protocol

Male salamanders were allowed to set up territories in experimental chambers (25×25×2 cm, Nunc bioassay dishes: Cole-Parmer, Vernon Hills, Ill.) for 5 days prior to a trial, which is sufficient time for them to establish territories (da Silva Nunes and Jaeger 1989). We then subjected each male (*n*=30) to three manipulations: (1) surrogate, (2) experimental (treated), (3) control (plain). The order in which the male residents experienced these manipulations was randomized, and no focal animal experienced the same intruder (see below) more than once (i.e., a randomized block design with the individual residents serving as the blocks). In order to minimize any effects that stress, due to handling, may have had on resident and/or intruder behavior in experiment 1, we placed both types of animals under a habituation dish for 15 min before data were recorded (da Silva Nunes and Jaeger 1989). After this habituation period, the 15-min experimental trial began. During this trial, the following variables were measured: (1) time spent in the ATR posture (threat: Jaeger 1984), (2) time spent in EDGE behavior (movement around the periphery of the arena while pushing against the roof or walls of the container as if trying to escape: Wise and Jaeger 1998), (3) number of nose taps (reception of olfactory cues that involves touching the nasolabial cirri to the substrate: Jaeger 1984; Dawley and Bass 1988, 1989), (4) the amount of time that the resident spent TOUCHing the stimulus (e.g., surrogate, experimental intruder or cotton swab, or control intruder or cotton swab), and (5) number of times that the resident bit the stimulus. For experiment 1, these variables were also measured for the intruding animals to test whether or not differential behavior patterns by experimental versus control intruders influenced the behavior of focal males. Both intruders (experiment 1 only) and residents were fed on days 2 and 4 during the establishment period of a trial. Because morphological asymmetries can influence the outcome of territorial interactions between red-backed salamanders (Wise and Jaeger 1998), we attempted to minimize such asymmetries between residents and intruders and between residents and source animals (see below) by keeping them within ±5 mm TL of one another.

Experiment 1: live intruder

The surrogate manipulation consisted of presenting each resident male (n=30) with a rolled piece of paper towel, moistened with spring water, approximately the size of an adult *P. cinereus*.

The experimental manipulation consisted of presenting each resident male salamander (n=30) with an intruder that had been swabbed with secretions from the opposite sex. There were two components to this manipulation: (1) the presentation of a female intruder swabbed with male secretions, and (2) the presentation of a male intruder swabbed with female secretions.

The secretions used in such swabs were taken from source animals. These source animals were also used as intruders but a source animal for one resident was not used as an intruder for that same resident in any of the subsequent manipulations. We made swabs, consisting of secretions from the following areas of the source animals' bodies: (1) underneath the chin, (2) the ventral part of the body, (3) the dorsal part of the body, (4) the exterior surface surrounding the postcloacal gland, because these body parts are thought to contain glands that produce chemicals associated with territorial defense (Simons and Felgenhauer 1992; Jaeger and Gabor 1993; Simons et al. 1994). These secretions were obtained from source animals and applied to treatment intruders via a moistened (spring water) cotton ball.

We are confident that the evaporation or displacement of source-animal secretions is unlikely for two reasons. First, courtship pheromones from *P. jordani* (a similar species from the same genus) are known to be "nonvolatile" (Rollmann et al. 1999). Second, Jaeger et al. (2002) found that male salamanders exhibited heightened aggression toward their pair-bond "partners" after such "partners" were placed in contact with a conspecific of the opposite sex and then re-introduced to their partner (the focal animal). Presumably, olfactory cues were the only way that these focal animals could distinguish between pair-bond "partners" that were or were not in contact with a conspecific of the opposite sex (Jaeger et al. 2002).

The control manipulation consisted of presenting a resident male salamander (n=30) with an intruder that had not been swabbed with secretions from the opposite sex. It consisted of two components: (1) a female intruder, and (2) a male intruder. Because the experimental manipulation consisted of handling the intruders in order to apply the secretions of the source animals, we attempted to neutralize stress due to handling in the control manipulation. Hence, control intruders were swabbed with cotton balls containing spring water prior to being presented to the residents. Three resident males escaped during experiment 1, which reduced our sample size to 27.

Experiment 2: no intruder

This experiment consisted of the same design as experiment 1 with the exception that cotton swabs containing the cutaneous secretions of red-backed salamanders, rather than live intruders, were presented to male residents (n=30). The manipulations for this experiment were presentation of a cotton swab containing: (1) spring water (surrogate), (2) secretions from a female, (3) secretions from a male, (4) mixed secretions from both sexes (experimental manipulation, treated). Each resident was tested once in each of the four treatments in random sequence. Behavioral response variables were as in experiment 1.

Accidentally, three animals that were used as focal males in experiment 1 were also used in experiment 2. The data from these animals were removed from experiment 2 to facilitate comparisons across experiments. However, we did analyze the data from experiment 2 with these three animals before dropping them from the analysis. Dropping these three animals had no effect on the significance of any variable or on the significance of any pair-wise comparison between the levels of any variable for the intra-experiment analysis.

Statistical analyses

We tested whether the times that male residents spent in (1) ATR, (2) EDGE, (3) TOUCH, and (4) number of nose taps differed among our manipulations via Friedman's analysis of variance by ranks for related data sets (Siegel and Castellan 1988). When P-values <0.05 were detected (via Friedman's ANOVA), we conducted sets of a priori contrasts that were calculated according to the algorithm in Silverstein (1978) to determine which manipulations were different from one another.

In experiment 1, the following contrasts were determined a priori to be biologically relevant: (1) female versus surrogate, (2) male versus surrogate, (3) male versus female, (4) treated female versus female, and (5) treated male versus male. In experiment 2, the following contrasts were determined to be biologically relevant: (1) female secretions versus surrogate, (2) male secretions versus surrogate, (3) female secretions versus male secretions, (4) female secretions versus male+female secretions, and (5) male secretions versus male+female secretions.

Because some intruders were used more than once in experiment 1, these data are not entirely independent. However, because of the extremely large number of intruders that we would have needed to ensure independence (90 of each sex), we limited our collection for ethical and practical reasons. We tested for differences in intruder behavior for times spent in ATR, EDGE, TOUCH, and number of nose taps using Kruskal-Wallis tests (Zar 1999). To address the issue of non-independence, we present two separate analyses. In the first, we present an analysis of the entire intruder data set (n=108). In the second, we present an analysis of the intruders that were used in only one trial (n=52). When differences in intruder behavior were detected, we used the multiple comparisons test for unbalanced data sets defined by Zar (1999) to detect differences among the treatments. There were not enough instances of biting across the manipulations in either experiment to allow for statistical analyses. Thus, we only report in which manipulations biting occurred.

In order to assess the effects of sensory modality (experiment 1 versus experiment 2), we developed a post-hoc scheme for statistical comparisons between experiments. Before comparisons for any variable were made, we tested the surrogate treatments of the two experiments for statistical differences via Mann-Whitney U-tests (Zar 1999) to determine if there were differences in resident baseline behavior between the two experiments. If the comparison of the surrogate treatments for a given variable yielded a P-value <0.100, then we terminated further analysis for the variable. However, if comparisons of the surrogate treatments for a given variable yielded a P-value >0.100, we concluded that experiment 1 and experiment 2 could be directly compared. When this occurred, we made comparisons between the following manipulations of the two experiments via Mann-Whitney *U*-tests: (1) male versus male secretions, (2) female versus female secretions, (3) treated male versus male+female secretions, (4) treated female versus male+female secretions.

All statistical tests, except for the a-priori contrasts and multiple comparisons tests, were conducted on StatView 5 (SAS Institute). A-priori contrasts for Friedman's ANOVAs and multiple comparisons for Kruskal Wallis tests were calculated by hand.

Adjustment of alpha

Because we present multiple statistical tests, we reduce α on an experiment by experiment basis (i.e. $\alpha/4$) via a sequential Bonferroni correction (Rice 1989). When we present inter-experiment comparisons, we adjust α for all tests (i.e. $\alpha/16$). In no cases do we attempt to correct for multiple comparisons (Zar 1999) or a-priori contrasts (Silverstein 1978) as both already control for the number of comparisons made. We also do not attempt to correct for analyses of intruder behavior as such analyses are designed to serve as indicators of relationships between intruder and resident behaviors.

Results

Experiment 1: live intruder

Based on the analysis of the full data set, intruders did not behave significantly differently for any variable across the manipulations (Table 1). However, the analysis of intruders that were used only once revealed a significant difference for time spent in ATR across treatments (Table 2). Nevertheless, none of our pair-wise comparisons detected significant differences in the time that intruders spent in ATR across the manipulations (Table 3). Intruders did not bite residents in any of the manipulations.

Residents did not differ significantly in the amount of time that they spent in EDGE, nor did they differ in the number of times that they nose tapped (Table 4). Upon the application of a sequential Bonferroni correction, there

Table 1 Kruskal-Wallis values and descriptive statistics for intruder behavior (full data set) from experiment 1. Live intruders were *F* female, *M* male, *TF* treated female, and *TM* treated male. All descriptive statistics are in seconds except for NT which is given in number of nose taps per trial

Variable	Manipulation	*n*	Median	Mean	Range	*H*	*df*	*P*
ATR (threat)						7.30	3	0.063
	F	27	72	101	462			
	M	27	169	222	569			
	TF	27	46	132	621			
	TM	27	107	160	631			
TOUCH						1.76	3	0.625
	F	27	27	58	227			
	M	27	13	50	330			
	TF	27	24	56	561			
	TM	27	10	45	278			
EDGE (escape)						0.32	3	0.956
	F	27	363	365	869			
	M	27	381	352	748			
	TF	27	346	370	768			
	TM	27	359	341	846			
NT (nose taps)						0.02	3	0.999
	F	27	4	8	23			
	M	27	5	10	41			
	TF	27	5	10	49			
	TM	27	6	9	36			

Table 2 Kruskal-Wallis values and descriptive statistics for intruder behavior (partial data set) from experiment 1. Live intruders were *F* female, *M* male, *TF* treated female, and *TM* treated male. All descriptive statistics are given in seconds except for NT which is given as number of nose taps per trial

Variable	Manipulation	*n*	Median	Mean	Range	*H*	*df*	*P*
ATR (threat)						8.79	3	0.032
	F	11	56	104	462			
	M	16	225	259	546			
	TF	10	66	149	621			
	TM	15	64	120	447			
TOUCH						0.336	3	0.953
	F	11	16	48	181			
	M	16	39	56	330			
	TF	10	31	53	141			
	TM	15	10	57	278			
EDGE (escape)						1.72	3	0.633
	F	11	443	406	677			
	M	16	387	372	733			
	TF	10	352	364	675			
	TM	15	307	303	805			
NT (nose taps)						3.38	3	0.337
	F	11	4	7	17			
	M	16	7	11	41			
	TF	10	9	15	49			
	TM	15	4	6	26			

Table 3 Multiple comparisons for time spent in ATR from the partial intruder data set of experiment 1. The pair-wise comparisons are *F vs M* female vs male, *F vs TF* female vs treated female, *F vs TM* female vs treated male, *M vs TF* male vs treated female, *M vs TM* male vs treated male, and *TF vs TM* treated female vs treated male (N.S. not significant at α=0.05)

Pair	*Q*	*P*
F vs M	2.34	N.S.
F vs TF	0.25	N.S.
F vs TM	0.01	N.S.
M vs TF	2.10	N.S.
M vs TM	2.56	N.S.
TF vs TM	0.28	N.S.

were no significant differences across the manipulations for time spent in ATR, and TOUCH (Table 4). Nevertheless, because our Friedman's ANOVAs for ATR and TOUCH yielded *P*-values <0.05, we calculated a-priori contrasts for these variables.

A-priori contrasts via Silverstein's (1978) technique for TOUCH yielded significant differences between the following pairs: female >surrogate and male >surrogate (cf. Tables 4 and 5). Likewise, contrasts for ATR yielded significant differences between the following pairs: male >surrogate and male >female (cf. Tables 4 and 5).

Residents bit intruders in the male (*n*=2), treated female (*n*=1), and treated male (*n*=3) manipulations.

Experiment 2: no intruder

No significant differences occurred in resident behavior across manipulations for TOUCH, EDGE, and number of nose taps (Table 6). However, a significant difference was detected for ATR (Table 6). Contrasts for ATR revealed significant differences between the following pairs: (1) male >surrogate, and (2) male >female (cf. Tables 6 and 7). Biting did not occur in any of the manipulations.

Table 5 A-priori contrasts via Silverstein's (1978) technique for residents in experiment 1: live intruder(*Sur-F* surrogate vs female, *Sur-M* surrogate vs male, *F-M* female vs male, *F-TF* female vs treated female, and *M-TM* male vs treated male; *n*=27 for all tests; *N.S.* not significant at α=0.05)

Variable	Pair	*Z*	*P*
ATR (threat)	Sur-F	0.56	N.S.
	Sur-M	3.72	<0.05
	F-M	3.16	<0.05
	F-TF	1.09	N.S.
	M-TM	1.09	N.S.
TOUCH	Sur-F	3.72	<0.05
	Sur-M	2.69	<0.05
	F-M	1.01	N.S.
	F-TF	0.23	N.S.
	M-TM	0.56	N.S.

Comparisons between experiments

Mann-Whitney *U*-tests did not detect significant differences for any of the comparisons made between experiments for ATR and EDGE (cf. Tables 8 and 9). For number of nose taps, the surrogate versus surrogate comparison yielded a *P*-value <0.100 (Table 8). We therefore terminated further inter-experiment comparisons for this variable. Significant differences in time spent TOUCHing the stimuli were detected for the

Table 4 Friedman's values and descriptive statistics for residents from experiment 1: live intruder (*F* female, *M* male, *TF* treated female, and *TM* treated male). Descriptive statistics are given in seconds except for NT which is given in number of nose taps per trial. No variables are significant upon the application of a sequential Bonferroni correction

Variable	Manipulation	*n*	Median	Mean	Range	χ^2	*df*	*P*
ATR (threat)						9.59	4	0.048
	Surrogate	27	42	68	318			
	F	27	43	76	269			
	M	27	113	259	836			
	TF	27	28	106	673			
	TM	27	68	121	498			
TOUCH						10.72	4	0.030
	Surrogate	27	0	13	137			
	F	27	16	29	119			
	M	27	6	31	181			
	TF	27	8	54	714			
	TM	27	19	36	297			
EDGE (escape)						3.01	4	0.542
	Surrogate	27	192	228	540			
	F	27	166	248	824			
	M	27	159	206	596			
	TF	27	262	286	818			
	TM	27	267	268	751			
NT (nose taps)						3.31	4	0.508
	Surrogate	27	6	10	40			
	F	27	3	5	22			
	M	27	3	5	20			
	TF	27	5	8	29			
	TM	27	5	7	25			

Table 6 Friedman's test values and descriptive statistics for resident behavior from experiment 2: no intruder. All descriptive statistics are given in seconds except for NT for which the units are number of nose taps per trial. The *P*-value still significant after the application of a table-wide sequential Bonferroni adjustment is denoted by *

Variable	Manipulation	*n*	Median	Mean	Range	χ^2	*df*	*P*
ATR (threat)						13.96	3	0.003*
	Surrogate	27	5	33	129			
	Female	27	10	50	249			
	Male	27	147	293	839			
	Treated	27	83	285	856			
TOUCH						1.59	3	0.661
	Surrogate	27	0	9	107			
	Female	27	0	10	220			
	Male	27	0	10	87			
	Treated	27	0	12	163			
EDGE (escape)						2.22	3	0.529
	Surrogate	27	104	198	774			
	Female	27	90	186	624			
	Male	27	141	183	705			
	Treated	27	190	245	763			
NT (nose taps)						4.78	3	0.189
	Surrogate	27	2	4	19			
	Female	27	5	9	63			
	Male	27	9	10	42			
	Treated	27	6	9	32			

Table 7 A-priori contrast results via Silverstein's (1978) algorithm for time (s) spent in ATR (threat posture) by residents (*S-F* surrogate vs female, *S-M* surrogate vs male, *F-M* female vs male, *F-T* female vs treated, and *M–T* male vs treated; *n*=27 for all tests; *N.S.* not significant at α=0.05)

Pair	*Z*	*P*
S-F	0.972	N.S.
S-M	4.55	<0.05
F-M	3.58	<0.05
F-T	2.16	N.S.
M-T	1.42	N.S.

following inter-experiment comparisons: (1) female versus female secretions, (2) treated female versus male+female secretions, (3) treated male versus male+female secretions (cf. Tables 8 and 9).

Discussion

Intruder behavior

Our analysis of the full intruder data set implies that intruder behavior did not differ by treatment for any variable. However, the partial analysis indicates that intruders differed across treatments for threat posture (ATR). Although our multiple comparison tests for intruder ATR (partial data set) do not detect differences for any pair-wise comparison, upon examination of Table 2 it is clear that the male treatment has much larger measures of central tendency than the other treatments. Thus, the lack of significance in our multiple comparisons tests is likely to be a type II error due to the internal reduction of α associated with such tests. (The null hypothesis of our Kruskal-Wallis test is that intruder behavior did not differ across any of the manipulations,

Table 8 Descriptive statistics and inter-experiment comparisons via Mann-Whitney *U*-tests. The *P*-value that is still statistically significant after the application of a sequential Bonferroni correction is denoted by * (*Exp. 1* Experiment 1, *Exp. 2* Experiment 2). The variable for which further analysis was terminated due to differences between surrogate treatments is denoted by +. Descriptive statistics for all variables except for nose taps are given in seconds. Descriptive statistics for nose taps are given as number of nose taps per trial

Variable/ comparison	*n* Exp. 1	*n* Exp. 2	Median Exp. 1	Median Exp. 2	Mean Exp. 1	Mean Exp. 2	Range Exp.1	Range Exp. 2	*U*	*Z*	*P*
ATR (threat)											
Surrogate	27	27	42	5	68	33	318	129	276.5	−1.56	0.118
Female	27	27	43	10	76	50	269	249	298.5	−1.16	0.245
Male	27	27	113	147	259	293	836	839	338.0	−0.46	0.646
TOUCH											
Surrogate	27	27	0	0	13	9	137	107	300.5	−1.30	0.194
Female	27	27	16	0	29	10	119	220	125.5	−4.46	<0.001*
Male	27	27	6	0	31	10	181	87	237.5	−2.44	0.015
EDGE (escape)											
Surrogate	27	27	192	104	228	198	540	774	307.5	−0.99	0.323
Female	27	27	166	90	248	186	824	624	303	−1.07	0.284
Male	27	27	159	141	206	183	596	705	343.5	−0.36	0.715
NT$^+$											
Surrogate	27	27	6	2	10	4	40	19	247.5	−2.04	0.041

Table 9 Descriptive statistics and inter-experiment comparisons via Mann-Whitney *U*-tests for the male+female secretions vs treated female and male+female secretions vs treated male comparisons. *P*-values that are still statistically significant after the application of a sequential Bonferroni correction are denoted by* (*Exp. 1* Experiment 1, *Exp. 2* Experiment 2, *TF vs M+F* treated female vs male+female secretions, *TM vs M+F* treated male vs male+female secretions). All descriptive statistics are given in seconds

Variable/ comparison	*n* Exp. 1	*n* Exp. 2	Median Exp. 1	Median Exp. 2	Mean Exp. 1	Mean Exp. 2	Range Exp.1	Range Exp.2	*U*	*Z*	*P*
ATR (threat)											
TF vs M+F	27	27	28	83	106	285	673	856	286.0	−1.38	0.166
TM vs M+F	27	27	68	83	121	285	498	856	322.5	−0.73	0.464
TOUCH											
TF vs M+F	27	27	8	0	54	12	714	163	160.0	−3.98	<0.001*
TM vs M+F	27	27	19	0	36	12	297	163	149.0	−4.14	<0.001*
EDGE (escape)											
TF vs M+F	27	27	262	191	286	245	818	763	322.0	−0.74	0.458
TM vs M+F	27	27	267	191	268	245	751	763	333.5	−0.54	0.589

and we rejected this null hypothesis for ATR in the partial analysis.) Therefore as a precautionary measure, for the remainder of the discussion, we do not assume that differences in agonistic resident behavior (ATR, experiment 1) are independent of agonistic intruder behavior (ATR).

It is also worth noting that differences in the intruders' behaviors may have reflected the responses of the intruders to the experimental manipulations. If this is the case, it poses a problem in the sense that it will further confound our ability to separate resident responses to intruder behavior from responses to the olfactory manipulations of experiment 1. However, an extreme form of this conundrum, in which residents responded to intruders' behaviors irrespective of the manipulations, is unlikely. The primary reason for this, as experiment 2 demonstrates, is that residents do utilize olfactory information to make decisions about how to behave toward conspecific stimuli. Furthermore, the statistical similarity between the ATR data from experiment 1 and experiment 2 provides little reason to assume that the residents ignored the olfactory information available in experiment 1 altogether.

Effects due to treatments

The repetitive pattern for threat display in resident behavior (ATR) (i.e., increased aggression towards untreated males and their untreated secretions relative to surrogates and females and female secretions) that we obtained across both experiments provides evidence that male residents displayed heightened aggression toward consexual stimuli and that this response was not dependent on the number of sensory modalities presented. Our direct inter-experiment comparisons of resident threat posture (ATR) further support this inference.

Although male residents showed reduced aggression when presented with treated male intruders (experiment 1), the result is non-significant, and male residents do appear to be able to identify treated females as female (i.e., residents were not "confused" by the treated female manipulation). This suggests that reduced aggression toward treated males (relative to plain male intruders), if it is not just an error in sampling, is a response to the reduced level of aggression that treated male intruders exhibited (relative to plain male intruders) toward residents, or vice versa.

When only olfactory information was presented (experiment 2), the level of aggression (ATR) exhibited by resident males in the male+female treatment is statistically intermediate to their response to male secretions and female secretions (treated mean=285 s, male mean=293 s, and female mean=50 s). Nevertheless, when male residents were presented with male+female secretions, they appeared to exhibit aggression levels more similar to those observed when they were presented with male secretions than when they were presented with female secretions. This may imply that males have more to lose from being too passive with an intruding male (i.e., loss of a territory) than from being overly aggressive with an intruding female (i.e., loss of a mating opportunity in an iteroparous species).

Effects due to sensory modality

Our inter-experiment comparisons imply that there are subtle but real differences between how resident males behaved when presented with bimodal information (experiment 1) versus unimodal information (experiment 2). In particular, male residents spent more time touching bimodal stimuli (male, female, treated male, and treated female intruders) than the analogous unimodal stimuli (cotton swabs containing male, female, and male+female secretions). Although the male versus male secretions comparison between experiments is not significant after the application of a sequential Bonferroni correction, the fact that four *P*-values <0.05 came from the same variable suggests that a type II error may have been committed (Moran 2003). These results imply that a visual encounter with an intruding conspecific, and perhaps most importantly the motion associated with such an encounter, are important for triggering "full-blown" touching responses in male residents.

Conclusions

Our results confirm the findings of Jaeger (1984) and Lang and Jaeger (2000) who showed that male red-backed salamanders are more aggressive toward consexual individuals than they are toward females. Our results also go further by demonstrating that this trend in aggressive behavior is not dependent on the presence of a live intruder, and that male olfactory signals alone are sufficient to stimulate heightened aggression in male residents. However, our data also demonstrate that male residents touched analogous stimuli more often when they contained both olfactory and visual information pertaining to sex than when they contained only olfactory information pertaining to sex.

Thus, while we report that resident male red-backed salamanders behave significantly differently in bimodal versus unimodal scenarios, our results provide no evidence that sensory modality affects red-backed salamanders' abilities to allocate aggression based on the association of sex (male vs female) with a stimulus. Hence, the generality of Rowe's (1999) claim (i.e., multimodal signals have superior discriminabilities) may not be applicable to territorial male red-backed salamanders that are attempting to identify the sex of an intruding conspecific.

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